Effect of acid deposition on soil animals and microorganisms: influence on structures and processes

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Soil biota in forests can be characterized by structural parameters such as species composition, species diversity, population abundances, biomass, spatial distribution patterns, phenology (cf. PETERSEN and LUXTON 1982, USHER 1985 for animals; KJØLLER and STRUWE 1982, SWIFT 1987, PAUL and CLARK (1989) for microfungi and bacteria). As the populations exhibit spatio-temporal dynamics, these parameters change in a stochastic and/or deterministic pattern. The zoo- and microbiocoenoses can be related to soil factors, vegetation types and to ecosystem processes. One example is the series mull - moder - mor (raw humus) (WALLWORK 1976; PETERSEN and LUXTON 1982; ELLENBERG et al. 1986; SCHAEFER and SCHAUERMANN 1989).

The majority of zoological analyses concerning the effects of acid immissions into forest soil deal with changes in the qualitative and quantitative composition of the animal community and its possible causes (cf. HAGVAR 1984; FUNKE 1986; summary in SCHAEFER 1985). This can be regarded as a "bioindicator" approach. On the other hand the effects of acidification on soil microflora are mainly analysed in studies on bulk parameters such as microbial biomass or activity (summary in WANG et al. 1980, FRANCIS 1986), studies on functional groups or biotic interrelationships are less well represented. Thus there is a deficit in process-orientated approaches (O'NEILL et al. 1986) analysing the effect of stress by acidification on soil biota-controlled ecosystem processes.

A conceptual framework of research on acid rain past and in future has to take into account three levels of analysis with increasing complexity: structure of the community, role of the biota in ecosystem processes and properties of the whole system (Fig. 1). I have to discuss one aspect of the problem in more detail: the present knowledge of the role of soil biota in ecosystem processes, mainly material flow (chapter 1). Then the analysis proceeds from a short evaluation of descriptional studies (chapter 3) to functional aspects (chapter 4 and 5) and the analysis of complex interactions (chapter 6). Emphasis is laid on some instructive examples.

1. Soil processes controlled by macro- and microbiota under quasi-stationary condition

A forest ecosystem can be divided into subsystems - the gas phase (CO_2, O_2), the solution phase (H_2O, dissolved ions) and the solid phase (living and dead organisms, dead organic material as products of decomposition, anorganic matrix of the soil). These components of the system can be aggregated or disaggregated to a diverse number of subsystems. The boundaries between them are regarded as interfaces. Flow of matter can be measured and quantified at the interfaces. Ecosystems in a quasi-steady state have balanced input/output relations of chemical flow. States of insta-

tionarity may occur due to aggradation, humus disintegration, build-up of a decomposer refuge, podzolization, deacidification or kryptopodzolization (ULRICH 1987, 1989).

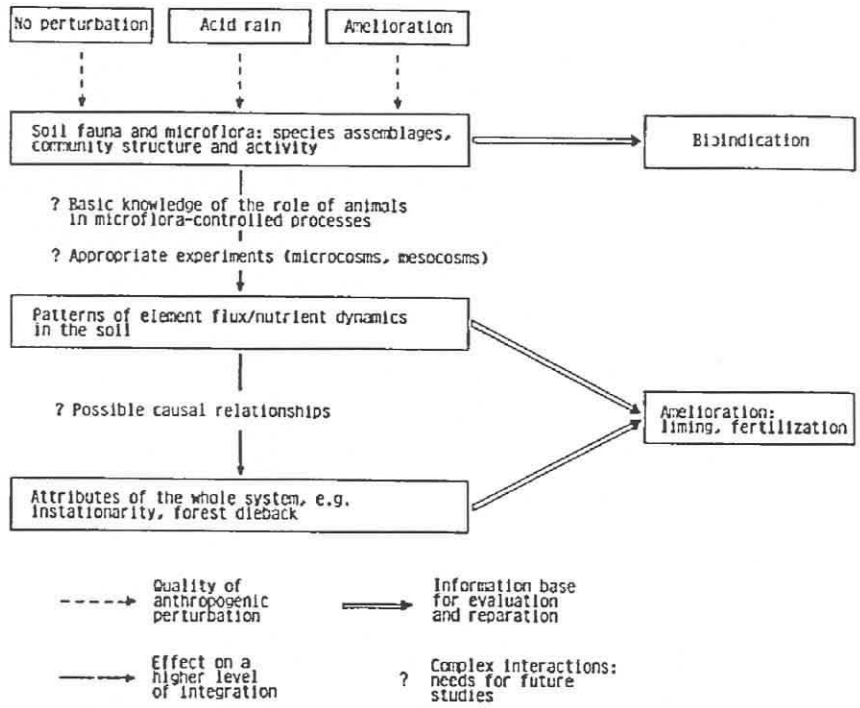
No perturbation
Acid rain
Amelioration
Soil fauna and microflora: species assemblages, community structure and activity
Bioindication
? Basic knowledge of the role of animals in microflora-controlled processes
? Appropriate experiments (microcosms, mesocosms)
Patterns of element flux/nutrient dynamics in the soil
? Possible causal relationships
Amelioration: liming, fertilization
Attributes of the whole system, e.g. instationarity, forest dieback
Quality of anthropogenic perturbation
Information base for evaluation and reparation
Effect on a higher level of integration
?
Complex interactions: needs for future studies

Fig. 1. Conceptual framework for the analysis of the effect of acid immissions on soil biota.

Organismic activity in the forest ecosystem manifests itself as flow of matter and/or energy and/or information. For the purpose of the review, the following assumptions about the role of soil biota in forest ecosystems are made (cf. Fig. 2). These assumptions may be partly regarded as hypothetical. However, much evidence has been accumulated in favour of them.

The transformation of organic material to inorganic nutrients within the decomposition subsystem is a prerequisite of chemical flow in the forest ecosystem.
Soil biota are controlling agents of the key processes in matter cycling (short-term immobilization, humification, mineralization/mobilisation) which determine the rate of nutrient release for primary producers.
Microfloral populations are responsible for processes such as C or P mineralization, ammonification, nitrification, denitrification, N fixation.
Animal populations act mainly as driving variables. Important faunal-microbial interactions are: comminution, modification and mixing of substrates, grazing on microbial populations, inoculation with microbial propagules.

The role of the soil fauna in matter cycling is principally understood. The direct contribution of animals to heterotrophic metabo-

lism is 1-15% (PETERSEN and LUXTON 1982). Element turnover (consumption) by a fauna of 10-15 g d wt m^{-2} can be equivalent to annual litterfall (SCHAEFER 1989). The macrofauna mainly effects mass loss of litter combined with bioturbation; mesofaunal and microfaunal groups as direct antagonists of the microflora are important for the mobilization and immobilization of nutrients. As an overall effect, the fauna tends to stimulate microbial activity (e.g. COLEMAN 1985; VISSER 1985; ANDERSON 1987, 1989; ANDERSON et al. 1985; SCHEU 1989; WOLTERS 1988, 1989b, WOLTERS et al. 1989).

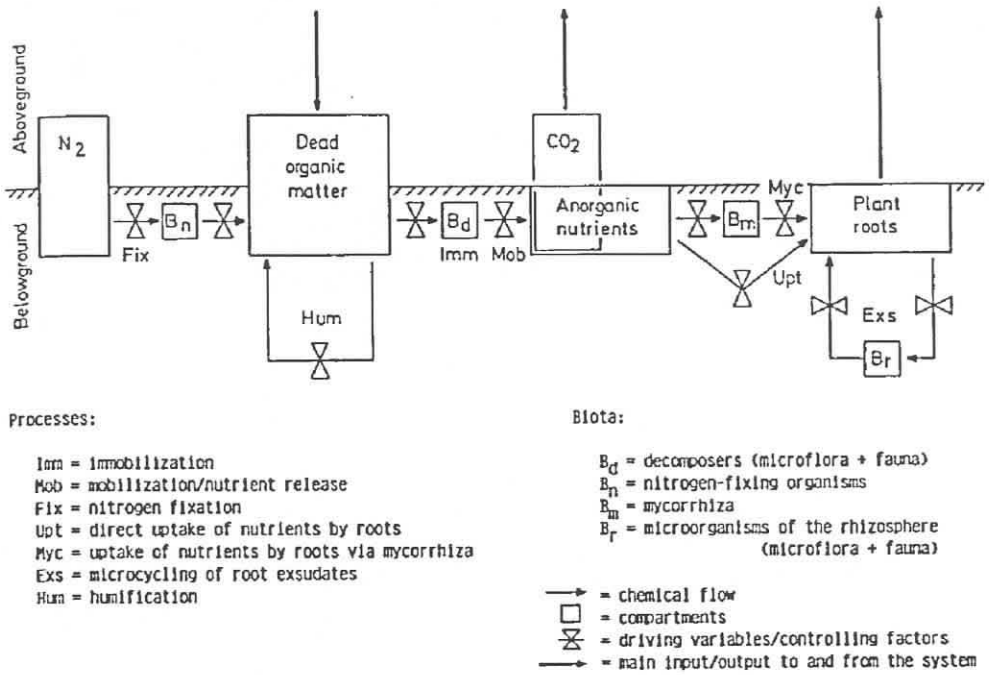

Fig. 2. Soil biota as controlling factors of ecosystem processes: element flux. Some processes are not included.

However, many reservations have to be made. Until now no unified theory on the function of soil biota in matter flow exists. Spatiotemporal scale and the influence of environmental variables (e.g. in the series mull - moder - mor (raw humus)) constitute main problems of analysis.

The litter-soil system is heterogeneous with components such as pedosphere, rhizosphere, mycorrhiza, dead wood. Phenomena on a microscale - e.g. microcycling as an effect of microbial-invertebrate interactions - cannot be quantitatively linked to ecosystem processes on a macroscale. ANDERSON (1987) even raises the question if interactions between invertebrates and microorganisms are noise or necessity for soil processes.

The influence of animals in the rhizosphere and in mycorrhizal symbiosis are poorly understood. Until now some tendencies emerge (COLEMAN et al. 1984; CLARHOLM 1985; NEWMAN 1985; FINLEY 1985; SHAW 1985). Microtrophic animals (Protozoa, Nematoda) tend to graze upon bacterial populations and contribute to nutrient re-

lease on a microscale. Mesotrophs (Collembola, Oribatida, Protura) tend to feed upon fungal mycelia with stimulation or inhibition of fungal growth and differential effects on nutrient uptake by roots.

2. Methods of analysis: descriptional and experimental design

Within the context of "effect of acid deposition on soil biota and their activity", different ecological situations are analysed or experiments designed:

Comparison of stands with different rates of acid immissions (e.g. FUNKE 1986). Special situations are different exposures: windward or leeward side of a mountain range (SCHAUERMANN, poster 133); litter-soil near the tree trunk base in comparison to the area below canopy (SCHÄFER, poster 132; POSER and SCHEU, poster 275; WOLTERS 1989a; SCHEU 1989).
Monitoring long-term changes within the ecosystem, such as soil fauna, litter accumulation or base status (SCHAUERMANN 1987; ULRICH 1987, 1989).
Experimental acidification/liming experiments in the field (HEILIGENSTADT et al., poster 274; cf. HAGVAR 1984; SCHAEFER 1985; many microbiolgial studies, cf. chapter 3, 4 and 5).
Experimental application of protons to systems in the laboratory, such as microcosms (SCHEU and WOLTERS, poster 276; WOLTERS, poster 277; WOLTERS and SCHAEFER, poster 278; many microbiological studies, cf. chapter 3, 4 and 5).

Further variables of the analysis are climatic region, height above sea level, tree species. Especially important is the soil type (mull - moder - mor (raw humus)): many of the soils affected by acid precipitation are already quite acid, a fact which together with concentration of acid input at the top of the profile renders soils sensible to stress.

In field studies it is often difficult to differentiate between effects of acidity, heavy metals or N-fertilization. In a top-down approach, complex laboratory systems have been proved to be suitable instruments to evaluate effects of acidic precipitation on soil biota.

3. Influence of acid deposition on zoocoenoses and microbiocoenoses

3.1. Fauna

Summaries of the effect of acid deposition on soil animals are given by HAGVAR (1984, 1987) and SCHAEFER (1985).

Among the high number of studies concerning the effect of proton input on the population parameters of soil animals, recent and more comprehensive analyses are presented by VAN STRAALEN et al. (1988) for a Dutch pine forest, by FUNKE (1986) and HARTMANN (1989) for South German spruce stands, by SCHAUERMANN (1987), HEILIGENSTADT et al. (poster 274) for North German beech and spruce forests. These and other studies had the following results as a reponse of the fauna to acidic inputs (for lack of space only a short, arbitrary selection of further references is given):

- Species numbers and species diversity values tend to decrease. This applies to the fauna of limnic habitats, too (SCHINDLER 1988; HEITKAMP et al., poster 352).
- The species composition of the community changes.
- Some species are depressed, some increase in numbers. A differential response can be observed even in groups of closely related species. Very high concentrations of protons tend to be generally inhibitory.
- As a very general tendency, species from the following groups (mainly belonging to the mesofauna) are favoured: Thecamoebae, Enchytraeidae, Oribatida, Uropodina, Collembola, Elateridae, some Diptera (e.g. Sciaridae). In contrast, species of the following groups (mainly of the macrofauna and microfauna) decrease: Protozoa (except Thecamoebae), Nematoda, Lumbricidae, Gastropoda, Isopoda, Myriopoda, Protura, other macroarthropods (e.g. Coleoptera), some Diptera.
- Consequently, more mull-like conditions develop into more moder-like conditions.

However, many reservations have to be made. As a general trend, significant changes in number, mass and composition of the soil animal community are effected only by inputs of higher proton concentrations often drastically surpassing real inputs in the field (SCHAUERMANN 1987). The effect of acid immissions depends on soil characteristics: For instance, in a moder soil acidification led to an increase of Enchytraeidae, a decrease of dipterans; however, enchytraeid worms were depressed, dipteran were favoured by acidification in a mull soil (SCHAUERMANN 1987; HEILIGENSTADT et al., poster 274).

Causal factors for the reaction of the fauna are: direct sensitiveness to protons or other chemical stress associated with acidification (e.g. decreased base saturation, reduced availability of cations, increased solubility of aluminum, iron and heavy metals, presence of nonacidic SO_4^{2-}, nitrogen inputs), change in reproductive success, alteration of the composition of the microflora (often favouring mycophagous groups of the mesofauna), alterations in the chemical content of leaf litter (presumably an important factor for the macrofauna), changes in microhabitat characteristics (e.g. compaction of pore space in a voluminous litter layer), shift in competitive relations and/or in predation pressure.

The response of the fauna to acid stress can be used as bioindication for deterioration of the system. For example, FUNKE (1986) parallels the decline of Protura numbers with damage of the tree mycorrhiza, because many proturan species feed upon ectomycorrhizal mycelia.

Case study: effect of acidification near tree trunks

Stemflow leads to an increased input of protons (and other air pollutants) in comparison to throughfall (ULRICH 1989). Soil acidity increases, litter accumulates (SCHÄFER, poster 132; POSER and SCHEU, poster 275).

In a mull soil of a beech forest, saprophagous macroarthropods (Diplopoda, Isopoda), enchytraeids, Collembola, Protura, dipterous larvae, predatory macroarthropods (Araneida, Chilopoda, Staphylinidae) reached higher densities near tree trunks than in

plots remote from trunks; generally, epedaphic species were favoured (POSER and SCHEU, poster 275; WOLTERS 1989a). The density of lumbricids was depressed near trunks, epigeic species clearly dominated (POSER and SCHEU, poster 275). The preference for the organic top horizon may be caused by rising acidity in the soil and the increased availablity of nutrients (such as Ca and Mg) in litter. The development into the direction of moder conditions may promote the disintegration of the litter layer and the mineral soil (WOLTERS 1989a).

3.2. Microflora

Methods of evaluating the effect of acid stress on the microflora mainly rely on bulk measurements of biomass or activity of the whole microflora (sometimes separately for bacteria and fungi) or on the analysis of microbially-controlled processes: biomass, FDA-active fungal biomass, carbon content, respiration, respiration after addition of glucose, ATP content, heat production (measured by microcalometry, REH et al., poster 286), soil enzymatic activity, concentration of leachates, ammonification, nitrification, denitrification, N-fixation, solubilization of P, solubilization of S, sulfate reduction.

Microorganisms in general are sensitive to acidity (BROSE et al., poster 287): microbial activity is inhibited by a direct H^+ effect and/or an indirect pH-induced effect such as increased toxic heavy metal availability (FRANCIS 1986). High nitrogen deposition may lead to a decrease in microbial biomass and/or activity (BERG, poster 130).

General tendencies for a response after acidification are (cf. reviews by TAMM 1976; WANG et al. 1980; RECHCIGL and SPARKS 1985; FRANCIS 1986):

Microbial biomass is depressed.
  Example: In a Scots pine forest FDA-active fungal mass decreased after acidification (BÅÅTH et al. 1984).
Shifts occur in the types of microorganisms that comprise the soil community (BÅÅTH et al. 1980).
  Examples: In a Scots pine forest the relative proportion of soil fungi (mainly Oidiodendron, Morteriella, not Penicillium) changed after acidification (BÅÅTH et al. 1984). In Adirondack forests species diversity of bacteria, actinomycetes and fungi was lower under acidic conditions (WANG et al. 1980).
Bacteria (except chemoautotrophic thiobacilli) are less acid tolerant than fungi, on the other hand fungi and actinomycetes increase population levels. One reason may be reduced competition by bacterial populations.
Ammonifying bacteria are not influenced.
Nitrifying bacteria are depressed.
Denitrifying bacteria are not very sensitive.
N-fixing populations are not significantly influenced.
Mycorrhizal symbiosis can be disturbed (SHAFER 1988; KOTHE, this volume; OBERWINKLER, pers.comm.).

Effects are mainly confined to the organic horizons and near-surface soil layers (KILLHAM et al. 1983). Little is known of the response of microbial populations in the rhizosphere.

It should be emphasized that studies demonstrate contrasting results. In many acidification experiments microbial activity was

not substantially impaired (WAINWRIGHT 1980). As a tendency, only very low ph values lead to measurable effects.

4. Influence of acid deposition on decomposition rate and carbon mineralization

Measuring changes in the carbon cycle, different parameters are concerned: mass loss of litter, soil respiration, incorporation of organic matter into the soil (bioturbation), degradation of definite types of substrates, activity of enzymes (e.g. dehydrogenase). The course of decomposition depends on the quality of litter (deciduous versus coniferous leaf litter, woody litter, belowground litter, artificially introduced substrates) and the soil environment (series mull - moder - mor (raw humus)). Naturally, decomposition rate is strongly related to microbial activity (see chapter 3.2.).

Many studies demonstrate a decrease of decomposition rate or soil respiration as a result of acidification (TAMM 1976; RECHCIGL and SPARKS 1985; FRANCIS 1986).

Some examples are presented:

First of all, long-term litter accumulation in forest stands (ULRICH 1989) or near tree trunks (POSER and SCHEU, poster 275) can be interpreted as inhibition of decomposition.

Litterbag experiments in damaged spruce stands demonstrated decreased decay rates in comparison to undamaged plots (HARTMANN et al. 1989). In Canadian pine stands, decomposition was inhibited in response to elevated levels of sulphur pollution near a gas plant (PRESCOTT and PARKINSON 1985). Atmospheric pollution from a coking plant reduced decomposition of Acer pseudoplatanus litter left in litter bags in soil at a depth of 2.5 cm by 35% compared with decomposition at a similar, but unpolluted, site (KILLHAM and WAINWRIGHT 1981).

Decrease of soil respiration induced by acid stress have been found by SCHÄFER (poster 132) for beech forests, by LOHM et al. (1984) for pine stands. CO_2 production decreased in pH-adjusted acid soils of an oak-pine forest (FRANCIS 1982). BÅÅTH et al. (1984) found lower soil respiration rates in a Scots pine forest after experimental acidification even in low concentrations. In vitro studies for coniferous litter showed that acidic conditions reduced microbial CO_2 evolution (MOLONEY et al. 1983).

Decomposition of special substrates may be inhibited. Some examples: Cellulose degradation in the top 10 cm of the soil near a coking plant was marginally inhibited by pollution (KILLHAM and WAINWRIGHT 1981). BEWLEY and PARKINSON (1986) found a reduced carbon mineralization rate in cellulose-amended mineral soil. GRANT et al. (1979) and STRAYER and ALEXANDER (1981) observed a lower mineralization rate of glucose under acidic conditions. The phase of rapid CO_2 evolution in protein hydrolysate-amended soil was delayed by acidification (GRANT et al. 1979).

Reduction in many soil enzymes (dehydrogenase, cellulase, amylase) have been reported for acidified soils (KILLHAM et al. 1983; FRANCIS 1986).

However, effects are not clear-cut. In many studies increased acidity did not influence the rate of carbon mineralization (ABRAHAMSEN et al. 1977; WAINWRIGHT 1980; cf. WILL et al. 1986); in some cases even an increase in weight loss in litter bags occurred (cf. FRANCIS 1986). It appears that inhibitory concentration have to be very high (around pH 2.0 or lower) to cause measurable effects. For instance, KILLHAM et al. (1983) observed inhibition of soil respiration only at a low pH value of 2.0.

5. Effect of acid deposition on microbial nutrient turnover

5.1. Nitrogen

Mineralization of nitrogen is hardly affected by input of acidified precipitation (WAINWRIGHT 1980; STRAYER et al. 1981, FRANCIS 1986, SCHÄFER, poster 132). This is mainly due to the low susceptibility of ammonification to acidity of the soil solution (TAMM 1976; STRAYER et al. 1981; KILLHAM et al. 1983; LOHM et al. 1984; RECHCIGL and SPARKS 1985), which may be caused by the heterogeneous structure of the microfloral populations involved. Some authors observed an increase of N mineralization after experimental acidification (WOLTERS, unpublished results).

In short-term experiments (TAMM 1976; WOLTERS, in prep.)) and in long-term studies (WAINWRIGHT 1980) it has been found that ammonification increases rather than decreases in acidified samples. Urease activity was unaffected at ph 3.0 in a ponderosa pine forest, pH 2.0 caused an inhibition (KILLHAM et al. 1983). Other authors (e.g. FRANCIS 1982) found lower rates of ammonification in acidified soils.

Generally, autotrophic nitrification is drastically reduced at low pH values (TAMM 1976; FRANCIS 1982, 1986; RECHCIGL and SPARKS 1985; PAPEN et al., poster 329). For NH_4-N-supplemented soils, BEWLEY and STOTZKY (1983) observed retardation of nitrification at pH 3.0, inhibition at pH 2.5. For different forest soils, nitrification of added ammonium (NH_4^+) was inhibited following continuous exposure to simulated acid rain of pH 4.1-3.2 (STRAYER et al. 1981). Hence, nitrogen turnover can be decreased (LOHM et al. 1984) and substantial amount of N might be accumulated in the forest soil. It should be emphasized that the inhibition of nitrification is not necessarily disadvantagous for the forest ecosystem because forest trees are not obligate nitrate plants and because less of the available nitrogen is turned into readily leachable nitrate, provided that enough available nitrogen is released during decomposition processes (TAMM 1976; FRANCIS 1986).

The rate of denitrification is rather slow in acidified soils (RECHCIGL and SPARKS 1985), and at greater acidities N_2O instead of N_2 is the predominant end product (FRANCIS 1982, 1986).

Asymbiotic N-fixing algae and bacteria appear to be especially susceptible to acid precipitation (CHANG and ALEXANDER 1983; FRANCIS 1982, 1986; RECHCIGL and SPARKS 1985). Generally, N gains by asymbiotic bacterial and fungal fixation may be insignificant in acid forests (TAMM 1976; ALEXANDER 1980).

5.2. Other nutrients

Microbial conversion of organic to inorganic forms of phosphorus in soils appears to be lower in more acidic environments (ALEXANDER 1980). Phosphatase activities being responsible for this conversion have generally been found to be decreased (KILLHAM et al. 1983) or unaffected or stimulated (WAINWRIGHT 1980; WILL et al. 1986). WILL et al. (1986) found a decrease of phosphatase activity at pH as low as 3.0. However, leaching of PO_4 from the soil may increase at high acidity (KELLY and STRICKLAND 1987).

Acidic soils degrade humus sulphur only slowly (ALEXANDER 1980; SIMON, poster 86). Arylsulphatase activities - involved in catalyzing the conversion of organic S to inorganic forms - generally are not influenced by acidic immissions (WILL et al. 1986) or are even increased in certain conditions (ph 3.0 in a ponderosa pine forest, KILLHAM et al. 1983). Leaching loss from the soil is increased at lower pH values (KELLY and STRICKLAND 1987). DAVID et al. (1982) assume that for North American hardwood and conifer sites in the Adirondacks Mountains sulfate formation by mineralization may be more important than exogenous inputs.

6. Influence of acid stress on interactions between animals and microflora

Only few studies are concerned with more complex multispecies systems in relation to acid immissions. It may be hypothesized that a decrease in faunal abundance/biomass leads to a decrease of microbially-mediated chemical flux, because animals tend to stimulate microbial activity (see chapter 1.). WOLTERS and SCHAEFER (poster 278) found for a moder soil that mesotrophic animals tend to intensify inhibition of carbon mineralization by grazing on an acid-stressed microflora. By suppressing fungal and bacterial populations through their grazing activities, animals were shown to inhibit N immobilization (VERHOEF et al., poster 134). Acid rain has a depressing effect on animal-induced mobilization of N in the litter layer leading to the accumulation of secondary organic compounds of microbial origin (WOLTERS and SCHAEFER, poster 278).

No experiments have been performed in vital microsites such as rhizospheres or the mycorrhiza-root system.

Case study: effect of acid immission on macrofaunal-microfloral interactions

In microcosm experiments it could be demonstrated that the presence of individuals of the soil macrofauna compensated acid-induced reduction of microbial repiration rate (SCHEU 1989). An 8fold increase of proton input into a beech mull soil led to a depression of carbon mineralization by 57%. This inhibitory effect could be reduced by comminution of litter by saprophagous macroarthropods and by the burrowing activity of earthworms. However, a complete buffering effect for the aciditiy-induced depression of microbial respiration was only possible by the translocation of the litter material into the soil by earthworms. Thus, acid-induced withdrawal of the fauna from the mineral soil would prevent buffering effects of the fauna and contribute to the development of a moder soil.

7. Effect of liming on soil biota and soil processes

Liming leads to changes in the composition of the soil animal community (summary in SCHAEFER 1985; PERSSON 1988). Recent, more comprehensive studies were performed for coniferous stands by FUNKE (1986), HUHTA et al. (1986), SCHAUERMANN (1985, 1987), JUDAS and SCHAUERMANN (poster 360), for beech forests by SCHAUERMANN (1985, 1987), HEILIGENSTADT and SCHAUERMANN (poster 272).

Generally, liming has a positive effect on groups of the macrofauna - lumbricids, isopods, millipedes and probably also on and molluscs. Further groups which tend to be favoured are: Nematoda, Protura, some predatory arthropods (e.g. Chilopoda). On the other hand densities of most oribatid mites, certain collembolan and enchytraeid species, dipteran (e.g. Sciaridae) as well as testate amoebae are found to be reduced by liming. FUNKE (1986) observed a general decrease in species numbers and abundance, the effect of liming was especially deleterious for enchytraeids and nematoceran dipterans.

In some cases factors responsible for the shift in relative proportions of the species appear to be direct influences of the increase in pH or Ca or Mg (HARTMANN et al. 1989; JUDAS and SCHAUERMANN, poster 360; HEILIGENSTADT and SCHAUERMANN poster 272); however, in many cases the "liming effect" is merely caused by changes in availabilty of food or in competition or in predation pressure (PERSSON 1988).

Liming increases carbon mineralization as a short-term effect (LOHM et al. 1984; MATZNER et al., poster 271; RINK et al., poster 284) and rates of nitrification (ABRAHAMSEN et al. 1977; IBROM and RUNGE, poster 270; MATZNER et al., poster 271; KREUTZER et al., poster 325; PAPEN et al., poster 329). However, raised microbial metabolism may lead to nitrogen immobilization and reduced net mineralization rates (IBROM and RUNGE, poster 270; RINK et al., poster 284).

Nitrogen fertilization (as NH_4NO_3 or urea) results in decreased soil microbial activity and biomass (SÖDERSTRÖM et al. 1983) and negatively affects the fauna (HUHTA et al. 1986; FUNKE 1986). In a Swedish pine forest, respiration rate, ATP content, and microbial biomass C decreased after N fertilization when expressed per gram C. This appeared to be an important factor in the observed increase in C content in fertilized plots (NOHRSTEDT et al. 1989). IBROM and RUNGE (poster 270) did not detect an effect of N-fertilization on N net mineralization in a beech forest (Solling).

Case study: Liming and faunal-microbial interactions

In a beech forest on moder soil (Solling) liming led to a development of the herb layer and to a drastic increase of earthworm numbers and biomass, the dominant species was Dendrodrilus rubidus, followed by Lumbricus rubellus and Dendrobaena octaedra. The soil profile changed from moder to mull-moder (as F mull) (HEILIGENSTADT and SCHAUERMANN, poster 272). MAKESCHIN (poster 327) observed an 18-19fold increase in earthworm mass after liming in a spruce forest; the micromorphology of the organic horizon

changed to structures dominated by worm casts. In pine forests, earthworms increased after liming, too (RINK et al., poster 284).

As microcosm experiments demonstrated, all three earthworm species of the limed Solling beech forest increased the mineralization of the freshly fallen beech leaves and effected an increase in the nitrogen contents of the soil solution. However, because they are not capable of mixing organic layer and mineral soil they cannot contribute to an increased stability of the system (WOLTERS and SCHAUERMANN 1989). A possible solution for this amelioration problem might be the introduction of anecic earthworm species (e.g. Lumbricus terrestris), connecting litter layer and soil (BEESE, SCHAUERMANN, unpubl. results).

Obviously caused by a shift from fungal to bacterial biomass, numbers of microphytophagous mesofauna groups (Oribatida, Enchytraeidae) and their associated predators (e.g. Araneida) decreased (HEILIGENSTADT and SCHAUERMANN, poster 272). Some groups (e.g. Oribatida) penetrated into deeper strata of the organic layers.

In microcosm experiments, WOLTERS (1988) observed for lime-ameliorated soil cores an irregular change between clear promotion and clear inhibition of decomposition of freshly fallen beech leaf litter by the presence of Mesenchytraeus glandulosus, in contrast to conditions in unchanged moder soil with significant stimulatory effects by the animals. In comparison to naturally base-rich mull soils, the humiphagous larvae of the elaterid beetle Athous subfuscus exert a negative effect on carbon mineralization of freshly fallen beech leaf litter in limed substrates of a moder soil, obviously because the microflora with a comparatively high metabolic quotient is strongly limited by the availability of carbon (WOLTERS 1989b). It appears that liming leads to labile equilibrium conditions with low buffering capacity of soil biota to external stress factors.

8. Conclusions

Principal effects of acid stress on the soil subsystem are: increase or decrease in faunal and microfloral populations, changes in species assemblages, overall reductions in several soil microbiological processes. How is the effect on an ecosystem level?

In a first step of analysis, some difficulties arise. Little is known about the effects of acidic rain on nitrogen transformation (e.g. ammonification, nitrification, denitrification) under field conditions (FRANCIS 1986). If at all, often only small effects of acidification on processes occur in the field. Additionally, animals tend to buffer negative effects on the decomposing microflora. Effects of acidification depend on characteristics of the soil environment, no simple generalizations are possible.

How are ecosystem attributes, which are connected to forest-dieback (review by WELLBURN 1988; ULRICH 1989), influenced by changes in the decomposer compartment? The crucial question is if changes in the activity of soil biota and their control of element flux contribute to the observed instationarity (lack of a steady-state condition) or instability (susceptibility to perturbations) of forest ecosystems. Some possible, admittedly very hypothetical, scenarios for the effect of acidification stress are:

Inhibition of decomposition leads to an accumulation of litter. A decomposer refuge builds up. The organic layer is more sensitive to stress. Immission and other disturbances may lead to humus disintegration and nitrate leaching (which indicates an equivalent proton release).
Inhibition of mineralization reduces the availability of plant nutrients. As a positive effect, inhibition of nitrification may lead to a decrease in nitrate leaching.
Decrease of the microfauna may cause disturbances of matter microcycling in the root zone.
Increase of the mesofauna may enhance the grazing pressure on mycorrhizal mycelia or even fine roots.
Decrease of the macrofauna (especially earthworms) lead to less bioturbation which impairs the buffer capacity of the litter and topsoil by preventing transport of material from deeper soil layers.

A general outcome of liming experiments is stimulation of decomposition and mineralization:

Increased nutrient availability could lead to increased productivity in nutrient limited stands; if mineralization occurs faster than nutrient uptake, then essential nutrients may be leached from the soil.
More irregular effects of animals on microbial activity may result in low stability of the soil-litter system and high liability to perturbations.

Future studies on the effect of acid rain, fertilization or liming on the decomposer subsystem of forests should concentrate on the following questions: the role of specific populations in mediating key nutrient transformations; the effect of the fauna on processes in the rhizosphere (short-cut chemical cycling, intrusion of root pathogens, formation and metabolic activity of mycorrhizae); influences of the abiotic soil environment on metabolic activity of soil organisms; development of experimental microcosm and mesocosm systems as a top-down methodological tool. It should be emphasized in this connection that the study of basic soil processes at quasi-stationary conditions are a prerequisite for greater insight into the responses of soils to perturbations.

9. Acknowledgements

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10. References

(Poster contributions at the congress are not included; they are referred to in the text by names of authors and number)

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